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# MADROÑO

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THE TAXONOMY OF THE SPECIES COMPLEX,  
STREPTANTHUS GLANDULOSUS HOOK.A. R. KRUCKEBERG<sup>1</sup>

The taxonomic delimitation of species and their infraspecific elements by experiment has nurtured a vigorous renaissance in biological taxonomy. Nevertheless, taxonomic revision has not been the sole objective of experimental studies of wild populations. Often, a revision may be merely a useful by-product of a study aimed at other objectives. The present review of the taxonomy of *Streptanthus glandulosus* Hook. came into being in such a fashion.

While investigating the extent of genetic isolation between certain populations of the central Californian serpentine species, *Streptanthus glandulosus*, the author discovered that genetic isolation between some populations was complete and between others only partial. Moreover it was observed that complete genetic isolation for such populations was often correlated with their geographic isolation and morphological distinctness. Here then were available three basic criteria for the demarcation of species. The presence of discontinuities in the variation pattern of *S. glandulosus* permits treating these biologically isolated populations as taxonomic entities. The experimental evidence for the taxonomic disposition of the members of the complex as species or subspecies is reported in detail elsewhere (Kruckeberg, 1957).

The taxonomy of the entities comprising the *Streptanthus glandulosus* complex has had a complicated history. The Hooker epithet of *S. glandulosus* was applied to plants collected by Douglas in California and remained the only taxon for the group until the time of E. L. Greene. Greene described twelve species within the *glandulosus* pattern of variation, eleven of which he placed in a new genus, *Euclisia* (Greene, 1906). Adopting more conservative views, Jepson (1925, 1936) and Abrams (1944) recognized only three species in the complex: *Streptanthus glandulosus* with two varieties [var. *albidus* (Greene) Jeps., and var. *pulchellus* (Greene) Jeps.], *S. niger* Greene, and *S. secundus* Greene. A recent reevaluation of *S. glandulosus* is found in an unpublished monograph of the section *Euclisia* by Morrison (1941). He recognized as the subsection *Pulchelli* of the section *Euclisia*, two species, *S. glandulosus* and *S. Coombsae* Eastwood. Morrison defined *S. glandulosus* broadly to include five subspecies: "*typicus*," *albidus*, *niger*, *pulchellus*, and *secundus*. This treatment of the complex accounted for the taxa recognized by Greene by treating certain of them as infraspecific elements of a polymorphic species complex and by relegating others to synonymy.

<sup>1</sup> A portion of this study was financed by grants from the state of Washington initiative No. 171 and the National Science Foundation.

Very little is known about *Streptanthus Coombsae*, since it has not been collected subsequent to its discovery in 1913 by Mrs. A. L. Coombs. Eastwood (1931) cited it as being collected "on the Williamson River, Southern Oregon." The only river in Oregon by this name is in the arid sagebrush country east of the Cascade Range in Klamath County, a most unlikely habitat for members of the section *Euclisia*, most of which occur on serpentine outcrops in cismontane California. However, members of the section *Euclisia* do occur in southwestern Oregon, growing on serpentine areas in Josephine County. *Streptanthus Coombsae* is not dealt with further in the present paper.

The present revision of the *Streptanthus glandulosus* complex is based on the premise that the degree of taxonomic relationship may be inferred from the degree of compatibility between different populations or from fertility of interpopulational hybrids. Accordingly, the taxonomic implications of hybrid fertility have been evaluated for over 300 artificial crosses involving 32 different population samples of the *S. glandulosus* complex in various combinations. The results and implications of this analysis were published by the author (Kruckeberg, 1957). Three of the eight taxa recognized here are regarded as species. These are *S. niger* Greene, *S. albidus* Greene, and *S. glandulosus* Hooker. In the previous treatments of Jepson, Abrams, and Morrison, *S. albidus* has been regarded as an infraspecific element of *S. glandulosus*. However, the sharp genetic discontinuity between *S. albidus* and all other populations, coupled with the morphological distinctness and regional restriction of *S. albidus* warrant the restoration of this Greeneian species. Similar justification can be made for the recognition of *S. niger*, a species of very narrow serpentine restriction. *Streptanthus glandulosus* is here taken as the most widespread and polymorphic of the three species. It occurs discontinuously and mainly on serpentine from Josephine County, Oregon to San Luis Obispo County, California. Three subspecies of *S. glandulosus* are recognized on the basis of more or less well-delimited morphological discontinuities and geographic range, coupled with high average inter- and infrasubspecific fertilities in interpopulational hybrids. They are *S. glandulosus* subsp. *glandulosus*, subsp. *pulchellus*, and subsp. *secundus* (with three varieties). Figure 1, taken from Kruckeberg (1956), summarizes the interrelationships of the major taxa constituting the *S. glandulosus* complex.

The elements taken here as constituting the *Streptanthus glandulosus* complex can be distinguished from other members of the section *Euclisia* by a particular ensemble of characteristics. The leaves are narrowly lanceolate and sinuately toothed to pinnatifid. The herbage is usually pubescent at least in the rosette stage, often densely hispid (*S. niger* is the only exception, with consistently glabrous and glaucous foliage). In contrast to the "color-spot" species where the terminal flowers of the raceme are sterile and their sepals highly colored and elongated, the members of the *S. glandulosus* complex produce solely fertile flowers which



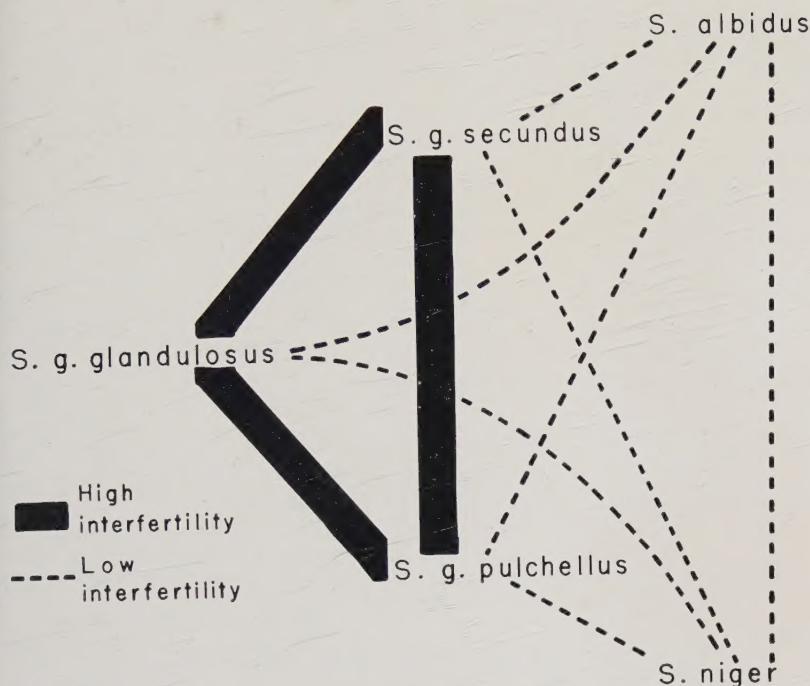


FIG. 1. Summary of the interfertility relationships among the five taxa of the *Streptanthus glandulosus* complex. A synthesis of pollen fertilities from over 300 artificial interpopulational hybrids.

become only slightly smaller towards the terminal flower. Thus the combined features of leaf shape, pubescence, and inflorescence serve to set the complex apart from other "euclisian" streptanthi. All members of the complex have the gametic chromosome number of 14.

A key to the five taxa permits the identification of the majority of populations. It must be recognized, however, that we are dealing with an intricate pattern of variation that appears to be correlated with the spatial isolation of populations (Kruckeberg, loc. cit.). In other words, the discontinuity of suitable habitats has promoted many morphologically distinct populations of a very local occurrence. Thus the eternal dilemma is forced upon us of either having to recognize taxonomically each Mendelian population or abstracting from the total variation pattern only the more salient representations. The latter course has been adopted here as best serving the needs of a practical taxonomy. At the same time attention is called to the fact that certain of the taxa (especially *S. glandulosus* subsp. *glandulosus* and *S. glandulosus* subsp. *secundus*) encompass systems of populations with variable morphology and showing varying degrees of genetic isolation.

KEY TO THE SPECIES AND SUBSPECIES IN THE *STREPTANTHUS GLANDULOSUS* COMPLEX

- A. Plants glabrous throughout; inflorescence simple or branched, forming a "zigzag" outline; pedicels twice as long as the purplish-black flowers; serpentine outcrops, Tiburon Peninsula, Marin County.....3. *S. niger*
- AA. Plants pubescent at least on the basal and lower cauline leaves; inflorescence straight and stiffly erect, simple or branched; pedicels shorter than the flowers.
- B. Inflorescence a second, simple or branched, raceme; Marin County and northward in the outer Coast Ranges to west-central Sonoma County.
- C. Sepals greenish-white, white, or yellow (or rarely rose); petals colored like the sepals or veined with rose or purple; inflorescence not crowded; plants usually tall, 3-7 dm. high; usually on serpentine, Marin and Sonoma counties, and possibly discontinuous northward along the outer Coast Ranges to Josephine County, Oregon.....1c. *S. glandulosus* subsp. *secundus*
- CC. Sepals reddish-purple; flowers crowded on the short inflorescences; plants usually dwarfish, 1-4 dm. high; on serpentine outcrops, south and east slopes of Mount Tamalpais, Marin County
- 1b. *S. glandulosus* subsp. *pulchellus*
- BB. Inflorescence not secund.
- D. Plants robust, 6-10 dm. tall; herbage coarse, often fleshy, glaucous and nearly glabrous; flowers either lilac-lavender or white; usually on serpentine, Alameda, Contra Costa and Santa Clara counties.
- E. Flowers greenish-white; on serpentine hills south of San Jose, Santa Clara County.....2a. *S. albidus* subsp. *albidus*
- EE. Flowers lilac-lavender; on barren outcrops of various parent materials, Alameda, Contra Costa, and Santa Clara counties.
- 2b. *S. albidus* subsp. *peramoenus*
- DD. Plants smaller, 3-7 dm. tall; herbage green, sparsely pubescent to hispid; flowers lilac-lavender to purple or purplish-black, rarely pale rose; widely distributed mainly on serpentine from San Luis Obispo County north to Tehama County.....1a. *S. glandulosus* subsp. *glandulosus*

1. *STREPTANTHUS GLANDULOSUS* Hook. Ic. Pl. 1, pl. 40. 1836.

Annual; stems erect, simple or divaricately branched just above the basal rosette, glabrous or sparingly (rarely densely) hispid to the inflorescence; plants densely rosulate at first, basal leaves 5-10 cm. long, hispid, narrowly lanceolate, tapering to a short, winged petiole, coarsely and sinuately toothed to shallowly pinnatifid, the teeth callus-tipped; cauline leaves sessile, auriculate, narrowly lanceolate, remotely toothed, gradually reduced upwards, becoming entire, auriculate, lanceolate-acuminate; by anthesis basal and lower cauline leaves becoming deciduous and stems ultimately naked up to 2-3 nodes below the inflorescence, flowers 0.8-1.2 cm. long, ascending to erect in single to several open, erect racemes; at anthesis flowers on wiry pedicels 1.0 cm. long, spaced at intervals of 4 to 2 cm. from base to apex; sepals glabrous or sparingly hispid, wholly or partly connivent, strongly keeled and collectively umbilicate at base, the calyx thus appearing inflated; petals well exerted; the crisped margins usually white, the upper pair with a broad blade, slightly to strongly recurved, longer than the lower, less recurved and narrower pair; stamens in three pairs, the upper with filaments connate to  $\frac{1}{2}$  -  $\frac{3}{4}$  their length, bearing sterile or scarcely polliniferous anthers,



the lower and lateral pair fertile, extending and dehiscing in that order, scarcely exerted; siliques glabrous (or rarely hispid), not torulose, 5–8 cm. long, straight and ascending, or divaricate, or arcuate or sharply reflexed; seeds oblong–oval, winged, 2–2.5 mm. long, 1.0–1.5 mm. wide; cotyledons accumbent (*vide* F. W. Hoffman).

1a. *STREPTANTHUS GLANDULOSUS* subsp. *glandulosus*. *S. glandulosus* Hook., Ic. Pl. 1. pl. 40. 1836. Type: *Douglas*, Monterey, California. *Erysimum glandulosum* O. Ktze., Rev. Gen. 2: 933. 1891. *Euclisia glandulosa* Greene, Leaf. Bot. Obs. 1: 82. 1904.

*S. biolettii* Greene, Pittonia 2: 225. 1892. Type: *Bioletti*, on Hoods Peak in 1889. *Euclisia biolettii*, Leaf. Bot. Obs. 1: 83. 1904.

*S. versicolor* Greene, Erythea 3: 99. 1895. Type: *Byxbee*, banks of Navarro River in 1894. *Euclisia versicolor*, Leaf. Bot. Obs. 1: 83. 1904.

*S. asper* Greene, Pittonia 3: 225. 1897. Type: *Greene*, on Mount St. Helena in 1894. *Euclisia aspera*, Leaf. Bot. Obs. 1: 83. 1904.

*S. bakeri* Greene ex. C. F. Baker, West Am. Plants, 2: 17. 1903. Type: *Baker*, near Bethany on plains of upper San Joaquin, 1903. *Euclisia bakeri*, Leaf. Bot. Obs. 1: 84. 1904.

*S. mildredae* Greene, Leaf. Bot. Obs. 1: 83. 1904. Type: *Holden*, Mount Hamilton. *Euclisia mildredae*, Leaf. Bot. Obs. 1: 83. 1904.

*Euclisia violacea* Greene, Leaf. Bot. Obs. 1: 83. 1904. Type: *Palmer*, "somewhere in middle California," 1876; *US* 4297!

*Euclisia elatior* Greene, Leaf. Bot. Obs. 1: 84. 1904. Type: *Vasey*, Santa Lucia Mountains, in 1880; *US* 4295!

Flowers lilac-lavender to purple, or more often purplish-black, rarely rose.  $n=14$ .

Type. "Monterey, California," *Douglas* as figured by Hooker (1836). Of the type, E. L. Greene (1904, p. 82) stated: "*S. glandulosus*, Hook . . . , as to original specimens, but figures false. *Streptanthus peramoenus*, Greene, . . . I did not believe that the plant with the remarkably irregular calyx described by me could be that which had been intended by Hooker's figure until I had seen the originals of *S. glandulosus* at Kew. Such falsification of the characters of a species is not publication; and this beautiful plant was truly first described, and therefore published, as *S. peramoenus*, which name ought to be continued in use, and Hooker's suppressed as being worse than a *nomen nudum*." However, Jepson evidently had no misgivings about the Hooker name when he annotated a specimen assigned to one of Greene's many segregates of subsp. *glandulosus* (i.e., *S. biolettii*) as follows: "Identical with *S. glandulosus* Hook.! Compared at Gray Herbarium with the cotype.—W.L.J." (UC 10874).

Range and Variation. The subsp. *glandulosus* constitutes the major element of the species and as such has the most extensive distribution. Within its north-south range from Tehama County to San Luis Obispo County, there may be blocked out areas of morphological homogeneity, although these are not always clear-cut. Plants with large, lilac-lavender

flowers on a thick-set peduncle occur in the southern end of the range—mainly in northern San Luis Obispo County. Northward from Monterey County, the transition is rather abrupt and the inflorescences are typically more delicate, with flowers that are either violet-purple or more commonly purplish-black. The blades of the petals are white along their crisped margins, with the median portion of the lamina veined in violet or purple. South of San Francisco Bay, the dark-flowered form of subsp. *glandulosus* is found chiefly on serpentine in Monterey, Santa Cruz, San Benito, and Stanislaus counties; a very few collections of this form are from southeastern Alameda County in the Bay region. North of the Bay, the distribution of the dark purple-flowered plants is mainly on serpentine outcrops in the mountains and foothills bordering the Great Valley, and occasionally westward to the outer Coast Ranges. This dark-purple form from north of the Bay has been collected most frequently in Napa and Lake counties, and to a lesser extent in eastern Sonoma, Solano, Colusa, Tehama, and Mendocino counties.

Specimens seen. San Luis Obispo County: 3.6 miles northeast of Valencia Peak, *Belshaw* 1727 (UC) (17)<sup>2</sup>. Monterey County: granite talus, east side of Henry Sands Canyon road, Gabilan Range, 2772 (UC) (5). Santa Cruz County: Charmichael's Mill, Santa Cruz Mountains, *Pendleton* 943 (UC) (1). San Benito County: trail above weather station, Pinnacles National Monument, Paicines, *Burgess* 172 (UC) (1). Stanislaus County: Del Puerto Canyon *Hoover* 3374 (UC) (3). Santa Clara County: Copernicus Peak, Mount Hamilton, *Sharsmith* 1287 (UC) (14). Alameda County: Mocho Creek, *Elmer* 4415 (UC) (2). Sonoma County: serpentine along ridge-top above Pine Flat and near Contact Mine, *Hoffman* 2902 (UC) (8). Napa County: Pope Creek bridge south of Walters Springs, *Keck* 2370 (UC) (11). Lake County: oak forest, Bartlett Mountain, 4 miles from Lucerne, *Mason* 11747 (UC) (24). Solano County: Weldon Canyon road north of Vacaville, *Gould* 262 (UC) (3). Colusa County: grade on Rumsey-Arbuckle road, *Hoover* 3205 (UC) (4). Mendocino County: serpentine talus 0.9 miles west of Hopland, *Hoffman* 2274 (UC) (4). Tehama County: 5½ miles west of Paskenta in foothills near a burn, *Baker* 12539 (UC) (1).

1b. *STREPTANTHUS GLANDULOSUS* subsp. **pulchellus** (Greene) Kruckeberg hoc loc. *S. pulchellus* Greene, Pittonia 2: 225. 1892. Type: *Howe*, dry ridges on the southern flank of Mount Tamalpais, 1892. *Euclisia pulchella*, Leaf. Bot. Obs. 1: 83. 1904. *Streptanthus glandulosus* var. *pulchellus* Jepson, Man. Fl. Pl. Calif. 420. 1925.

Plants often dwarfish, 1–4 dm. tall, flowers reddish-purple, usually secund, crowded on the short, simple to branched racemes; siliques divaricate or ascending, 4–6 cm. long.  $n = 14$ .

<sup>2</sup> One specimen for each county is cited; the total number seen from a given county is given in parentheses.



Range and Variation: Subspecies *pulchellus* is confined to serpentine outcrops on the slopes of Mount Tamalpais, Marin County. The combination of dwarfish stature, purple flower color and second inflorescence serves to distinguish subsp. *pulchellus* from the other subspecies. It is, however, highly interfertile with the Marin County populations of subsp. *secundus*, as well as with certain Napa and Lake County populations of subsp. *glandulosus*. Two other species of the section *Euclisia* occur in Marin County. With *S. niger*, subsp. *pulchellus* is both spatially and genetically isolated. With the equally narrow endemic, *S. batrachopus* Morrison, it is sympatric, but as yet no attempt has been made to cross these two very different plants.

Specimens seen. Marin County: Large serpentine outcrop between Mountain Theater and the toll road, Mount Tamalpais, *Morrison 3103* (UC) (21).

1c. STREPTANTHUS GLANDULOSUS subsp. **secundus** (Greene) Kruckeberg hoc loc. *S. secundus* Greene, Fl. Fran. 261. 1891. Type: *Greene*, north base, Mount Tamalpais, 1886. *Euclisia secunda* Greene. Leaf. Bot. Obs. 1:83. 1904.

Flowers in open or crowded second racemes; siliques usually arcuate, 5–6 cm. long.

1d. STREPTANTHUS GLANDULOSUS subsp. SECUNDUS var. **secundus**. *S. secundus* Greene, Fl. Fran. 261. 1891. *Euclisia secunda* Greene, Leaf. Bot. Obs. 1:83. 1904. (*Greene*, north base, Mount Tamalpais.)

Flowers greenish-yellow, tinged with rose or purple as blotches at the base of the sepal and on the veins of the petal lamina.  $n = 14$ .

Range. Mostly on serpentine, north side of Mount Tamalpais and the adjacent grassy or chaparral-covered hillsides of Marin County.

Specimens seen. Marin County: Serpentine slope at head of Lucas Valley, *Howell 13945* (WTU) (13).

1e. STREPTANTHUS GLANDULOSUS subsp. SECUNDUS var. **sonomensis** Kruckeberg hoc loc. *Hoffman 2323* (UC 985963) serpentine, Great Eastern Quicksilver Mine, near Guerneville, Sonoma County, June 8, 1948.

Floris luteis vel viridio-alba vel alba.

Flowers yellow, white or greenish-white.  $n = 14$ .

Range. On serpentine or other ecologically similar sites in central Sonoma County, ranging from the eastern border of the county (west end of Knight's Valley) to Cazadero in the western section of the county.

Specimens seen. Sonoma County: 3 miles south of Monte Rio on road to Camp Meeker, *Hoover 5084* (UC) (24).

1f. STREPTANTHUS GLANDULOSUS subsp. SECUNDUS var. **hoffmanii** Kruckeberg hoc loc. *Constance 2155* (UC 614606) moist soil of steep, rocky, nonserpentinized bank with *Umbellularia* and *Aesculus* at edge of Sequoia grove, 400 feet altitude, Russian Gulch, 8 miles south of Fort Ross, Sonoma County, April 24, 1938.

Floris roseis vel roseo-purpureis.

Flowers rose to rose-purple.  $n = 14$ .

Range. Open, rocky slopes of either serpentine or non-serpentine parent material. Known from only the type locality and Red Slide at the headwaters of Austin Creek, both areas just back of the wooded ridges along the coast.

Specimens seen. Sonoma County: serpentine, Red Slide at headwaters of East Austin Creek, *Hoffman* 2343 (UC) (3).

Range and Variation of subsp. *secundus*. Subspecies *secundus* occupies a well-defined territory extending from the north side of Mount Tamalpais, Marin County, north throughout most of Sonoma County. The flowers of the Marin County plants (var. *secundus*) have greenish-white calyces and yellowish petals, but with both sets of parts prominently veined with violet, while the flowers of the Sonoma County plants (var. *sonomensis*) are either pure yellow or greenish-white. The center of distribution of subsp. *secundus* appears to be just north and south of the Russian River around Guerneville, where it occurs predominantly on serpentine, as var. *sonomensis*.

The rose-colored plants (var. *hoffmanii*) have been collected only rarely in the little explored Russian Gulch-Austin Creek areas north of the Russian River. The collections of the enthusiastic *Streptanthus* specialist, Freed W. Hoffman, of Guerneville, have added materially to our knowledge of the flora of this little known region. Variety *hoffmanii* has the most delicate inflorescences of all the forms of *S. glandulosus*, a character easily singled out in garden cultures where it can be compared with the inflorescences of plants from other populations. As was pointed out in Kruckeberg (1956), the high interfertility of this form with Sonoma and Lake County plants of both subsp. *glandulosus* and subsp. *secundus*, make it difficult to place these rose-colored populations in one or another of the subspecies. The second inflorescence and the distribution of the variety justify its alliance with subsp. *secundus* here.

The recognition of two regional facies of the subspecies, one in Marin County (var. *secundus*) and the other in Sonoma County (var. *sonomensis* and var. *hoffmanii*), is supported by the fact that interpopulational hybrids between plants from the two areas are less fertile than those involving populations within the two areas.

Populations in Josephine County, Oregon, which are readily referable to the *S. glandulosus* complex, are, nevertheless, anomalous in their relation to subspecies *secundus* and *glandulosus*. These plants from Oregon most resemble the Marin County variety of subsp. *secundus*. Yet the gap in distribution of subsp. *secundus* between even the northern Sonoma County plants and the southern Oregon ones is both absolute and wide. Hybrids between the Oregon plants and plants of Californian *S. glandulosus* do not clarify the affinity of the Oregon plants to one or another of the three subspecies, since exceptionally fertile hybrids have been obtained in a number of these crosses. The taxonomic position of the Oregon plants



will remain in doubt until collecting of streptanthi throughout the serpentine of northern California and southwestern Oregon is intensified and until the fertility of the appropriate interpopulational hybrids is evaluated.

2. STREPTANTHUS ALBIDUS Greene, Pittonia 1:62. 1887.

Habit similar to *S. glandulosus*, but usually taller (6–10 dm. high), stout, tending to be fleshy and glaucous throughout; rosette leaves sinuately dentate, callus-tipped, sparsely pubescent, or more commonly, glabrous, broadly linear-lanceolate, 9–12 cm. long; cauline leaves similar but gradually shorter upwards, saggitate-clasping; flowers large, 1.4 cm. long (between distal ends of reflexed upper and lower petals) and 1.7 cm. wide; petals strongly recurved, the margins of the blade crisped and usually white; siliques straight, stiffly and divaricately ascending, 6–8 cm. long; seeds as in *S. glandulosus*.

2a. STREPTANTHUS ALBIDUS Greene subsp. **albidus** *S. albidus* Greene, Pittonia 1:62. 1887. Type: *Rattan*, hillsides four miles south of San Jose, in 1887. *Euclisia albida*, Leaf. Bot. Obs. 1:83. 1904. *S. glandulosus* var. *albidus* Jepson, Man. Fl. Pl. Calif. 419. 1925.

Sepals greenish white, tawny purple-tinged at base.  $n = 14$ .

Specimens seen. Santa Clara County: Metcalfe Canyon,  $1\frac{1}{4}$  miles northeast of Coyote, *Sharsmith* 3956 (UC) (8); photograph of isotype seen.

2b. STREPTANTHUS ALBIDUS Greene subsp. **peramoenus** (Greene) Kruckeberg hoc loc. *S. peramoenus* Greene, Bull. Torrey Club 13:142. 1886. Type: *Bolander*, in Oakland Hills.

Sepals lilac-lavender. Plants tending to be less robust than subsp. *albidus*.  $n = 14$ .

Specimens seen. Alameda County: Oakland Hills, *Michener & Bionetti* 672 (WTU) (5). Contra Costa County: 2 miles outside the north entrance to Mount Diablo State Park, *Morrison* and *Constance* 3030 (UC) (7). Santa Clara County: 0.3 miles southwest of Madrone, *Belshaw* 16167 (UC) (2).

Range and Variation of Species. *Streptanthus albidus* occurs on serpentine and ecologically similar sites in Alameda, Contra Costa and Santa Clara counties. Its robustness, the glabrous and glaucous herbage, combined with the flower color are its marks of distinction. It is here taken to include two distinct color variants. The lilac-lavender flowered subsp. *peramoenus* is found in the Oakland-Berkeley Hills, Mount Diablo, the hills above Sunol and the ridges of western Santa Clara County (e.g., upper Stevens Creek). Subspecies *albidus*, with greenish-white flowers is confined to the serpentine foothills south and east of San Jose around Coyote and Madrone. The two subspecies are fully interfertile and yet both are genetically isolated from all other members of the *S. glandulosus* complex.

3. *STREPTANTHUS NIGER* Greene, Bull. Torrey Club 13:141. 1886. *Euclisia nigra*, Leaflet Bot. Obs. 1:83. 1904. Type: *Greene*, Point Tiburon, 1886.

General habit of *S. glandulosus*; herbage glabrous, glaucous-green throughout; plants simple or branched above the base, 2–8 dm. high; basal leaves lanceolate in outline, pinnately lobed, 5–7 cm. long; inflorescence open, the rachis “zig-zag”; pedicels 1.4–2.0 cm. long, twice as long as the flowers; sepals purplish-black with a distinct metallic cast, 0.7 cm. long; calyx appearing inflated, umbilicate based, the sepals strongly carinate; petals linear, the margins white and crisped, the median portion of the lamina veined purplish-black, exserted only 2–3 mm., barely reflexed; filaments of the upper pair of stamens connate almost throughout, their anthers wholly sterile; lateral and lower pairs of stamens barely exserted, crowded in the contracted throat of the corolla, through which the flat capitate stigma is forced; siliques stiffly ascending, straight, 5–6 cm. long; seeds oblong to oval, narrowly winged, 1.6–1.8 mm. long.  $n = 14$ .

Range and Variation. *Streptanthus niger* has never been found elsewhere than the type locality, on the southern tip of Tiburon Peninsula, Marin County, an area of not more than a square mile in extent. The plant is found in draws, slopes and ridges of the hilly area of the peninsula just above the narrow Raccoon Straits between the peninsula and Angel Island. The entire area is of stony, shallow soil derived from serpentine rock, and apart from the wholly barren spots, supports a varied and rather dense herbaceous vegetation, with only a very few and widely separated specimens of stunted *Umbellularia* and *Quercus*. The single population of *S. niger* is made up of small, semi-isolated colonies, with no apparent variation within or between colonies. It may well be, then, one of the most narrowly restricted species in the Californian flora.

As shown in figure one, hybrids between *S. niger* and any other member of the complex have been sterile. Thus, genetic isolation is complete between *S. niger* and even the most likely relatives of the species such as *S. glandulosus* subsp. *pulchellus* which grows on nearby Mount Tamalpais, or *S. albidus* subsp. *peramoenus* which occurs in the Berkeley Hills just across San Francisco Bay.

Specimens seen. Marin County: Rocky serpentine soil, Tiburon, *Raven* 843 (UC) (6).

Close relationship between the *S. glandulosus* complex and other streptanthi may be sought among other members of the section *Euclisia*, particularly the so-called “color-spot” species, aptly delimited by Morrison (1941) as the subsection *Insignes* (in his unpublished thesis). Hybrids between one of the *Insignes* group (*S. insignis* Jeps.) and *S. albidus* were quite fertile. *S. hispidus* Gray, another member of the *Insignes* group, appears to be related to *S. glandulosus* subsp. *pulchellus*. The author intends to expand the interfertility studies in *Streptanthus* to include other species of the genus, especially those in the section *Euclisia*.



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## STUDIES OF THE POLLEN GRAIN AND POLLEN TUBE IN CERTAIN MALVACEAE

R. M. DATTA

The pollen grains of all Malvaceae in which they have been studied are round with spinescent outgrowths of varying shapes and lengths distributed uniformly on the exine wall (Wodehouse, 1935; Zander, 1935; Lang, 1937; Erdtman, 1952). A varying number of roundish conspicuous apertures is distributed evenly upon the exine surface. Concerning these apertures, Wodehouse (1935) remarks, "Though their shape and their function of serving as places of exit for the pollen tube prompt us to call them germ pores, there is much evidence to show that such apertures are morphologically furrows, which have become so shortened that they coincide in extent with their enclosed germ pores."

Amici (1830), the discoverer of the pollen tube, recorded polysiphonous germination of the pollen grain in *Hibiscus Trionum* and *H. syriacus*; in the latter species, some grains gave rise to twenty to thirty tubes. Guignard (1904) corroborated him after *in vivo* studies of *H. Trionum*, and found that only one tube plays a part in fertilization. Stenar (1925) found

in *Althaea rosea* ten tubes per grain, and in *Malva neglecta*, fourteen. Lang (1937) found five to ten tubes per grain produced by *Anoda cristata* and *Lavatera cachmeriana*, *in vitro*. Iyenger (1938) reported two tubes per grain in diploid Asiatic cotton (*Gossypium herbaceum*) and in tetraploid American cotton (*G. hirsutum*). He concluded that the frequency of two tubes is greater in the tetraploid American types than in the diploid Asiatic ones, and noted branching of the tubes, in the styles only. He noted polysiphonous germination also in *Hibiscus vitifolius*. Purewall and Randhawa (1947) found pollen grains of *H. esculentus* to germinate thirty minutes after they were placed in culture media. They grew more rapidly in culture media than under moist conditions. As many as six tubes were produced from some grains; branching of the tubes occurred both in culture media and on stigmatic surfaces.

The purpose of the studies here reported was to confirm and extend the foregoing observations.

#### ACKNOWLEDGMENTS

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#### MATERIALS AND METHODS

The seventeen species, varieties, or races, upon which studies were made, are listed in Table 1.

A medium for *in vitro* studies was prepared as follows: 0.5 g. powdered agar agar and 1.0 g. sucrose were dissolved in 25 cc. boiling water. After cooling to 35°C., 0.5 g. powdered gelatin was added and dissolved by stirring. The mixture was filtered through muslin into test tubes plugged with cotton and was sterilized by suspending the tubes in boiling water for several minutes.

Drops of this medium were smeared on clean slides by the technique used in making blood films. The slides were dusted with pollen grains from flowers immediately after anthesis and placed in moist chambers consisting of large Petri dishes.

For *in vivo* studies, flowers were emasculated and bagged. On the following morning they were pollinated from fresh flowers of the same species. After 30–45 minutes, the styles were fixed in acetic-alcohol (1:1). On the following day they were transferred for storage to 70 per cent alcohol. When they were to be examined, they were boiled briefly in lactophenol, cooled, stained for 5 minutes in 1 per cent acid fuchsin, and squashed on the slides.



Studies of the sterility of pollen of *Hibiscus cannabinus* (the American race), *H. radiatus*, and *H. Sabdariffa*, were made late in November of 1954, when the two former species were near the end of their flowering season. Temporary mounts of the pollen of each species were made in aceto-carmine. Stained and unstained grains were counted. The diameters of fifty grains of each species were determined.

#### OBSERVATIONS

When one or more tubes grow forth from a grain, they contain at first hyaline cytoplasm which shows rapid circulatory movement. Afterwards, starch granules start flowing out of the pollen grain, gradually and ultimately packing up the pollen tubes, with their branches and ramifications, if present and making them turgid. When stained with iodine-potassium-iodide solution, the tubes become deep blue in color.

The tube nucleus and the generative cell or sperms are found in only one tube from a particular grain. As in the generality of pollen tubes, the tube nucleus lies nearer the tip than the generative cell. The generative cell follows the contour of the tube, but the tube nucleus sometimes bulges out slightly. Germination within the anther loculi, which has been observed in the tiliaceous genus *Corchorus* by Datta, 1956, has not been observed in Malvaceae.

Our observations on the occurrence of multiple and branching pollen tubes are given in Table 1.

The pollen grains of *Abutilon Theophrasti*, *Urena lobata*, and *Althaea rosea* failed to germinate under the conditions provided; those of *Abutilon Avicennae* germinated *in vitro*, but not within one half hour on the stigmas. In *Hibiscus esculentus*, germination was notably rapid, occurring *in vitro* within about five minutes at any period of the day; this shows that the grains remain viable throughout the day; and growth of the tubes was so rapid as to be easily perceived with the low power of the microscope.

Germination through more than one aperture was observed in every species in which germination took place, with the exception of *Malachra capitata*.

Branched pollen tubes were observed in *Hibiscus vitifolius*, *H. esculentus*, *H. Sabdariffa*, *H. populneus*, *H. cannabinus* (the Indian, Ibadan, and Nigerian races, but not the American) and in  $F_1$  hybrids of *Hibiscus radiatus* and *H. cannabinus*. They were not observed in any of the other species. Since *Hibiscus cannabinus* (Indian) shows branching of the pollen tubes while *H. radiatus* does not, the appearance of this character in the hybrid suggests that it may be dominant.

Pollen of *Hibiscus radiatus* and *H. cannabinus* collected near the end of their period of flowering showed a low percentage of fertility, while *H. Sabdariffa*, still in full flower, was producing pollen of high fertility (Table 2). Ferguson (1924) and Kostoff (1932) have found the age of flowers to affect the fertility of pollen.

TABLE 1. Observations of germination of pollen grains, and of multiple and branching pollen tubes in certain Malvaceae, with references to the illustrations.

Species	Largest number of tubes observed from one grain		Branching	Illustrations
	<i>in vitro</i>	<i>in vivo</i>		
<i>Hibiscus vitifolius</i>	11	6	rare	Figs. 8, 9
<i>H. esculentus</i>	26	12	profuse	Figs. 1, 2, 3
<i>H. Sabdariffa</i>	9	8	frequent	Fig. 4
var. <i>altissima</i>	3		none	
<i>H. radiatus</i>	6		none	
<i>H. populneus</i> ( <i>Thespesia populnea</i> )	5		rare	
<i>H. cannabinus</i> (Indian)	11	17	slight	Figs. 5, 6, 7
<i>H. cannabinus</i> (Ibadan)	9		rare	
<i>H. cannabinus</i> (Nigeria)	5		rare	
<i>H. cannabinus</i> (American)	8		none	
<i>H. radiatus</i> × <i>H. cannabinus</i> (F <sub>1</sub> plants)	4		rare	Fig. 12
<i>Abutilon Avicennae</i>	3	no germination	none	
<i>A. Theophrasti</i>	no germination	no germination	none	
<i>Sida rhombifolia</i>	2	2	none	Fig. 10
<i>Malachra capitata</i>	1	2	none	Fig. 11
<i>Urena lobata</i>	no germination	no germination		
<i>Althaea rosea</i>	no germination	no germination		

The average diameter of pollen grains of *H. Sabdariffa* as we have determined it, namely 127.9 $\mu$ , is distinctly smaller than as reported by Lang (1937), namely 145.5 $\mu$ .

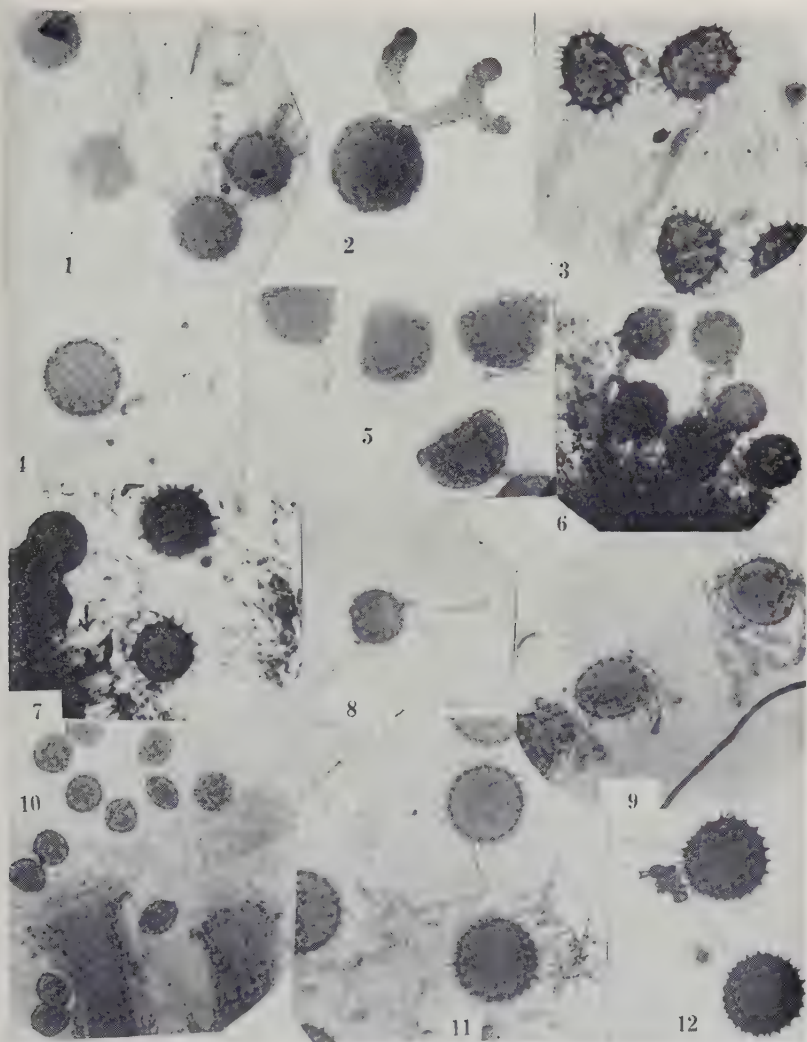
TABLE 2. Observations of fertility and dimensions of pollen grains of three species of *Hibiscus*.

Species	Number of pollen grains examined	Number of stained grains	Number of non-stained grains	Percentage sterility	Range of diameters	Average diameter of 50 grains
<i>H. radiatus</i>	383	179	204	53.26	98.4–139.4 $\mu$	120.96 $\mu$
<i>H. cannabinus</i>	450	163	287	63.76	131.12–188.6 $\mu$	153.5 $\mu$
<i>H. Sabdariffa</i>	396	353	43	10.86	98.4–147.6 $\mu$	127.9 $\mu$

## SUMMARY

Production of pollen tubes from more than one aperture of the pollen grain has been observed in *Hibiscus vitifolius*, *H. esculentus*, *H. Sabdariffa* and its variety *altissima*, *H. radiatus*, *H. populneus*, *H. cannabinus*, first generation hybrids of *H. cannabinus* and *H. radiatus*, *Abutilon Avicennae*, and *Sida rhombifolia*.





Figs. 1-12. Germination of pollen of Malvaceae: 1, 2, *Hibiscus esculentus* *in vitro*; 3, *H. esculentus* *in vivo*; 4, *H. Sabdariffa* *in vivo*; 5, *H. cannabinus* (Indian) *in vitro*; 6, 7, *H. cannabinus* (Indian) *in vivo*; 8, *H. vitifolius* *in vitro*; 9, *H. vitifolius* *in vivo*; 10, *Sida rhombifolia* *in vivo*; 11, *Malachra capitata* *in vivo*; 12,  $F_1$  hybrid of *H. radiatus*  $\times$  *H. cannabinus* *in vitro*.

Branched pollen tubes have been observed in *Hibiscus vitifolius*, *H. esculentus*, *H. Sabdariffa*, *H. populneus*, *H. cannabinus* (Indian, Ibadan, and Nigerian races), and first generation hybrids of *H. cannabinus* and *H. radiatus*.

Low fertility of pollen observed in *H. cannabinus* and *H. radiatus* is believed to have been caused by lateness of season.

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### A NEW SPECIES AND SOME NOMENCLATURAL CHANGES IN *SOLANUM*, SECTION *TUBERARIUM*

DONOVAN S. CORRELL

In 1852, Dunal described *Solanum lycopersicoides*, no named because of its close resemblance to some of the species in the genus *Lycopersicon*, the common garden tomato. Sometime between 1909 and 1914, Weberbauer collected a plant in an undesignated locality in Peru which, though quite different, superficially resembled *Solanum lycopersicoides*. Again, in 1925 Pennell obtained the same plant at Quive in the Department of Lima.<sup>1</sup> Until now, no apparent attempt was ever made to identify these collections. This distinctive plant is here named in honor of the latter

<sup>1</sup> Since preparing this manuscript, Earl E. Smith, Ramón Ferreyra and I found a solitary sterile plant above Canta in the Department of Lima, Peru, on March 7, 1958.

collector, an unassuming and scholarly gentleman who will long be remembered for his work on the family Scrophulariaceae.

These two species belong to Series Juglandifolia in Subsection Hyperbasarthrum of Section Tuberarium, characterized by being somewhat woody non-tuber-bearing plants with yellow stellate or rotate-stellate corollas, and pedicels that are articulate above the very base. Because these two species appear to stand alone as the closest links between *Solanum* and *Lycopersicon*, they are both here treated for convenience in comparing their individual characteristics.

Leaflets suborbicular, coarsely crenate; pedicels articulate well below the middle or near the base ..... *S. pennellii*  
 Leaflets irregularly pinnatifid; pedicels articulate less than 3 mm. below the calyx. .... *S. lycopersicoides*

***Solanum pennellii*** sp. nov. Herba habitu *S. lycopersicoidei* similis, omnino glanduloso-pubescent, ramosa; folia imparipinnata; foliola petiolulata, suborbicularia, crasse crenata, basi truncata vel cordata; inflorescentia terminalis vel ramos laterales terminans, corymbosa vel racemosa; pedunculus bracteis singulis vel pluribus semiorbicularibus aliquando in inflorescentiam procurrentibus ornatus; pedicelli multo infra medium vel prope basim articulati; flores flavi vel lutei; corolla lobis late ovatis, acutis vel subobtusis rotato-stellata; antherae diadelphicae, supra medium valde curvatae; stylus pilis longis sericeis ornatus, prope apicem valde curvatus; ovarium globosum.

Plant woody-herbaceous, erect, 5 dm. or more tall, glandular-pubescent throughout, rootstock unknown but doubtless non-tuber-bearing; stem woody; leaves odd-pinnate, up to 13 cm. long, with few interstitial leaflets, the leaflets 5 or 7, prominently petiolulate, suborbicular, coarsely crenate, truncate to cordate at base, up to 4 cm. in diameter; petiolules up to 1 cm. long; pseudostipular leaves shaped similarly to the leaflets but somewhat reniform, 1-2 cm. long; inflorescence terminal or terminating the lateral branches, corymbose or racemose, few- to many-flowered; peduncle slender, up to 8 cm. long, provided with one or more semiorbicular bracts that sometimes continue into the inflorescence; pedicels slender, up to 2 cm. long, articulate well below the middle or near the base; flowers lemon-chrome; calyx 5-6 mm. long, divided to near the base into oblong-elliptic obtuse lobes; corolla rotate-stellate, up to 3.5 cm. in diameter, the lobes broadly ovate and acute to subobtuse; anthers of two lengths, linear-oblong in outline, the largest up to 10 mm. long, the smaller up to 7 mm. long, strongly recurved above the middle, opening by two pores at the apex that soon become slit to the base of the anthers, the filaments rather thick, up to 2 mm. long; style up to 11 mm. long, strongly curved near the apex, adorned with long silky hairs for most of its length; stigma elongate and prominent; ovary orbicular; fruit unknown but probably orbicular.

Specimens examined. PERU. Department of Lima, Quive, open rocky



slope, herb, corolla "lemon chrome," alt. 800–1000 m. ("plant ascending to 2500 m."), June 9, 1925, *F. W. Pennell 14304* (type, PH, sheet no. 642829); Peru, 1909–1914, *Weberbauer 5315* (without other data) (F, no. 627894); Peru, hanging from cut along road above Canta, Department of Lima, 2,850 m. alt., plant branching from a woody rootstock, no flowers or fruits present, March 7, 1958, *Correll, Smith & Ferreyra P287* (LUNDELL).

*SOLANUM LYCOPERSICOIDES* Dunal in DC. *Prodromus* 13 (1):38. 1852; Bitter, *Repert. Sp. Nov.* 11:466. 1912; Ochoa, "Agronomía" 18 (74): 13–16. 1953.

Plant bushy, glandular-pubescent throughout, up to 2.5 m. tall, non-tuber-bearing; stem woody, erect or tortuously ascending; leaves asymmetrically pinnate-pinnatifid, up to 13 cm. long, with numerous toothed interstitial leaflets, the leaflets 7 to 11, sessile to decurrent on the rachis or rarely shortly petiolulate, irregularly pinnatifid, up to 5 cm. long, with the pinnules often toothed and the ultimate segments obtuse to acute; pseudostipular leaves lobed similarly to the leaflets, about 1 cm. long; inflorescence terminal, subterminal or terminal on the branches, corymbose, many-flowered; peduncle rather stout, 4–9 cm. long; pedicels slender, up to 12 mm. long, articulate 1–2 mm. below the calyx; flowers bright yellow, showy; calyx 3.5–5.5 mm. long, divided to about the middle into ovate to ovate-lanceolate acute to acuminate lobes; corolla rotate-stellate, about 2 cm. in diameter, with short triangular lobes, coarsely pubescent on the outer surface; anthers 3.5–5 mm. long, oblong-elliptic in outline, opening by two large pores at the apex that commonly become longitudinal slits on the inner surface extending from apex to base, the filaments filiform, 1–2 mm. long; style 7–12 mm. long, slender, pubescent below, with a conspicuously clavellate stigma; fruit orbicular, about 6 mm. in diameter, purple-black, marked with green.

Specimens examined. PERU. Department of Tacna: Cordillera de Palca, *A. D'Orbigny 291* (type collection, P, MPU); Cordillera de Palca, 1851, *Weddell* (P); Quebrada de Palca, *von Tschudi* (W); Prov. Tarata, open hillside among lava boulders, alt. 2900 m., bush 2–2.5 m. high, calyx yellow-green, corolla bright yellow, fruit purple-black and green at base, April 25, 1942, *Metcalf 30404* (G, MO, US); Prov. Tarata, near Candarave, dry open hillside, in clay soil and volcanic rock, 2800 m. alt., bush 0.7–2 m. tall, calyx green, corolla yellow, fruit green and black at base, April 15–25, 1942, *Metcalf 30382* (G, MO, US); Causiri, a un kilómetro mas arriba de Palca y a 45 klmts. de Tacna, March 20, 1953, *Ochoa 2035* (GH, US).

Although these two species are closely allied, they differ from each other in the shape of their leaflets as well as in their floral characters. The sub-basal articulation of the pedicels of *S. pennellii* in contrast to the sub-apical articulation of those of *S. lycopersicoides* is distinctive. Although the anthers of both species eventually split to the base at anthesis, those of *S. pennellii* have at first prominently marginate terminal pores while



FIG. 1. *Solanum*. A *Solanum lycopersicoides*, upper part of plant, D'Orbigny 291;  
B. *Solanum pennellii*, upper part of plant, Weberbauer 5315.

the anthers of *S. lycopersicoides* appear never to have well defined terminal pores. In fact, many of the species in Section *Tuberarium* have anthers that are split to the base, although this process may be considerably delayed. The weak tissue below the apical pores is frequently easily ruptured.

These two species are living evidence in support of those who would combine *Solanum* and *Lycopersicon*. They are true representatives of a transition between these two genera. The lack of an apical sterile tip to the anthers, however, traditionally place them in *Solanum*, although the anthers of both are commonly split their entire length as in *Lycopersicon* and both closely resemble in habit some of the species in that genus. Furthermore, Rick (in Proc. Nat. Acad. Sci. 37 (11):741-744. 1951) has demonstrated that *Solanum lycopersicoides* can be hybridized with *Lycopersicon esculentum* Mill.

***Solanum hougassii*** Correll nom. nov. *Solanum verrucosum* Schlecht. var. *spectabilis* Correll, U. S. Dept. Agr., Agr. Monogr. No. 11:228, figs. 164-166. 1952. *Solanum spectabile* (Corr.) Hawkes, Ann. and Mag. Nat. Hist., ser. 12, vol. 7:701. September, 1954; Swaminathan and Hougass, Am. Jour. Bot. 41:650. October, 1954 (as *S. spectabilis*), non *S. spectabile* Steudel, Nomenclator Botanicus, ed. 2, pt. 2:606. 1841.

The above authors, Hawkes, Swaminathan and Hougass, independently came to the same conclusion regarding the proper status of this plant. Apparently sensing a need for urgency, they published their results within a month of one another. Unfortunately, in elevating the variety to a specific category a homonym resulted. It is a pleasure to rename this Mexican species for R. W. Hougass, the able and congenial project leader for the Inter-regional Potato Introduction and Preservation Project at Sturgeon Bay, Wisconsin.

***Solanum nelsonii*** Correll nom. nov. *Solanum confusum* Correll, U. S. Dept. Agr., Agr. Monogr. No. 11:63, figs. 41-42. 1952, non *S. confusum* Morton, Contr. U. S. Nat. Herb. 29:70. 1944.

At the time of publishing my work on *Solanum* in 1952, the Gray Index to which I referred was, unknowingly to me, not up to date. This accounts for the publication of this homonym. This species, a native of Oaxaca, Mexico, is here renamed in honor of E. W. Nelson who collected the type specimen.

The author, who is in the process of classifying and coordinating all data regarding the species in the Section *Tuberarium* of *Solanum*, is indebted to the Agricultural Research Service, United States Department of Agriculture and National Science Foundation, as well as to Texas Research Foundation, for continuous support and encouragement in the pursuance of this difficult problem, of which this is a part.

Texas Research Foundation,  
Renner, Texas



## DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See Madroño 9: 257-258, 1948)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
POLYGONACEAE				
<i>Eriogonum inflatum</i> Torr. & Gray	n = 16	D. Stone & P. Raven UC <sup>1</sup>	Raven 10850 UC	Road to Panoche, San Benito County, Calif.
SCROPHULARIACEAE				
<i>Castilleja breviloba</i> Piper	n = 12	L. R. Heckard ILL	Heckard 267 JEPS	Northeast of Gasquet, Del Norte County, Calif.
<i>chromosa</i> A. Nels.	n = 12	L. R. Heckard ILL	Bacigalupi (& Heckard) 4252 JEPS	Northwest of Baldwin Lake, San Bernardino Mts., San Bernardino County, Calif.
<i>*inflata</i> Pennell	n = 36	L. R. Heckard ILL	Heckard 800 JEPS	Point Reyes light- house, Marin County, Calif.
<i>integra</i> A. Gray	n = 12	L. R. Heckard ILL	P. C. Silva, 29 Aug. 1955 JEPS	19 miles east of Springville, Apache County, Ariz.
<i>linariaefolia</i> Benth.	n = 12	L. R. Heckard ILL	Mason 14563 JEPS	East of Campito Mt., White Mts., Mono County, Calif.
<i>pilosa</i> S. Wats.) Rydb.	n = 12	L. R. Heckard ILL	Bacigalupi 4295 JEPS	Franktown, Washoe County, Nev.
<i>roseana</i> Eastw.	n = 12	L. R. Heckard ILL	Bacigalupi (& Heckard) 4052, 4053 JEPS	City Creek Canyon, San Bernardino Mts., San Bernardino County, Calif.
<i>roseana</i> Eastw.	n = 12	L. R. Heckard ILL	Heckard 493 JEPS	Lewis Creek Road, Monterey County, Calif.
<i>stenantha</i> A. Gray	n = 12	L. R. Heckard ILL	Bacigalupi (& Heckard) 4085 JEPS	Potrero Creek, near Barrett Junction, San Diego County, Calif.
COMPOSITAE				
<i>Bidens laevis</i> (L.) B. S. P.	n = 11	A. M. Torres UNM	Torres 52 UNM	Bernalillo County, New Mexico
<i>Borrichia arborescens</i> (L.) DC.	2n = 28	R. T. Neher IND	Heiser 3195 IND	Dade County, Florida

\* Prepared slide available.

<sup>1</sup> Symbols for institutions are those listed by Lanjouw and Stafleu, Index Herbariorum, Part I. Third Edition, 1956, Utrecht.

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
<i>frutescens</i> (L.) DC.	2n = 28	R. T. Neher IND	Heiser 3205 IND	Manatee County, Florida
<i>Simsia</i> <i>grandiflora</i> Benth.	n = 17	C. B. Heiser IND	Heiser R7 IND	San Salvador, Salvador
<i>polycephala</i> Benth.	n = 17	C. B. Heiser IND	Heiser R5 IND	Antigua, Guatemala
<i>Thelesperma</i> <i>intermedium</i> Rydb.	n = 8	A. M. Torres UNM	Torres 12 UNM	Bernalillo County, New Mexico
<i>longipes</i> Gray	n = 10	A. M. Torres UNM	Torres 18 UNM	Otero County, New Mexico
<i>megapotamicum</i> (Spreng.) Kuntze	n = 11	A. M. Torres UNM	Torres 10 UNM	Socorro County, New Mexico
<i>subnudum</i> Gray	n = 12	A. M. Torres UNM	Torres 23 UNM	San Juan County, New Mexico

## APOMIXIS IN THE GRAMINEAE. TRIBE ANDROPOGONEAE: HETEROPOGON CONTORTUS

W. H. P. EMERY AND W. V. BROWN

*Heteropogon contortus* (L.) Beauv. ex Roem. & Schult. consists of a relatively uniform series of populations with an extensive native range throughout most of the tropical and sub-tropical grassland regions of the world. In parts of the Hawaiian Islands, Australia, Indo-Malaya, India, Asia Minor, Africa, Europe, and the Americas it forms an important part of the range forage. The species is both palatable and nutritious, but when mature the plants produce fertile spikelets which have a sharply pointed callus and a stout hairy awn. These spikelets may penetrate the skin or lining of the digestive tract (Pammel, 1911), causing severe irritation and infection. They may even affect the general health of grazing animals (Chippindall, 1954).

Previous cytological studies of *H. contortus* from various parts of the world have shown that many of the populations which comprise this species are characterized by highly irregular meiotic divisions. Gould (1956) reported that some irregularities were observed in meiotic divisions of the pollen mother cells (PMC's) in six collections from Texas and northern Mexico. Mehra (1954) examined six collections from India and reported varying numbers of univalent, bivalent, trivalent, and quadrivalent configurations in the microsporocytes of each collection. On the other hand, Celarier and Harlan (1953) examined collections from Tanganyika, India, Australia, and Madagascar and noted a high degree of irregularity in the

PMC's of the first three, but an almost regular division in the PMC's of the collection from Madagascar.

Evidence for the existence within the species of a polyploid series, with occasional aneuploid forms, appears well-substantiated by a number of workers (Brown, 1951; Celarier and Harlan, 1954; Darlington and Janaki-Ammal, 1946; de Wet, 1956; Gould, 1956; and Mehra, 1954). The chromosome counts reported in 22 different collections of *H. contortus* range from  $2n=20$  to  $2n=80$ , with modes at  $2n=40$  and  $2n=60$ . The irregularity of meiotic divisions, and the existence of an extensive polyploid series of chromosome forms, suggested the possibility of apomixis in this species.

### MATERIALS AND METHODS

Seed from thirty collections were obtained through the generous cooperation of Dr. R. P. Celarier of the Oklahoma Agricultural Experiment Station and Dr. E. J. Britten of the Hawaii Agricultural Experiment Station. Flowering material of twelve American collections was provided through the cooperation of Dr. F. W. Gould of Texas Agricultural and

TABLE 1. CULTURES OF HETEROPOGON CONTORTUS EXAMINED<sup>1</sup>

CULTURE NO.	PLACE OF ORIGIN	2n	CULTURE NO.	PLACE OF ORIGIN	2n
A-4595-1	Galton, Australia	....	A-3729-4	Southern Rhodesia	....
A-4595-3	Galton, Australia	....	A-3050-2	Madagascar	40
A-3962	Borgar, Java	40	A-3050-3	Madagascar	40
A-2667	New Delhi, India	40	G-683	Monterrey, Mexico	60
A-5293	Delhi, India	....	G-730	Durango, Mexico	...
A-5298	India	....	G-788	Parral, Mexico	....
A-2668	Coimbatore, India	40	G-847	Chihuahua, Mexico	60
A-3230-3	Allahabad, India	40	G-420	Cuauhtemoc, Mexico	....
A-4829	Dehra Dun, India	....	G-384	Chihuahua, Mexico	60
A-3703-1	Belgian Congo	40	G-500	Durango, Mexico	....
A-3703-2	Belgian Congo	40	G-1485	Durango, Mexico	....
A-3703-3	Belgian Congo	40	G-1556	Coahuila, Mexico	....
A-3234	Kenya	40	G-874	Encino, Texas	....
A-3729-1	Southern Rhodesia	....	G-873	Encino, Texas	....
A-3729-3	Southern Rhodesia	....	.....	Artesia Wells, Texas	....
			.....	Marathon, Texas	....

<sup>1</sup> Voucher specimens for all collections utilized in this study will be deposited in the University of Texas Herbarium. Collections bearing the prefix "A" are also deposited in the Oklahoma State University Herbarium, Stillwater, Oklahoma, and were obtained through the cooperation of that institution. Those with the prefix "G" were provided by the Texas Agricultural and Mechanical College. The plants from Artesia Wells and Marathon, Texas, are collections of the authors.



Mechanical College. The authors wish to express their thanks to these men, as well as to all others who were instrumental in assembling seed from the foreign collections of this species.

Plants of fifteen non-American cultures (7 Indian, 4 African, 1 from Madagascar, 2 Australian, and 1 from Java) were established in our grass nursery together with two collections from Texas.

Collections utilized in the embryological examination of *H. contortus*, together with their place of origin, are given in Table 1. Flowering material at various stages of development was killed and fixed in Navashin's fluid. Pistils were dissected from the florets, dehydrated in butyl-ethyl alcohol, embedded in Tissuemat, sectioned at 8 to 12 microns, and stained in Delafield's hematoxylin.

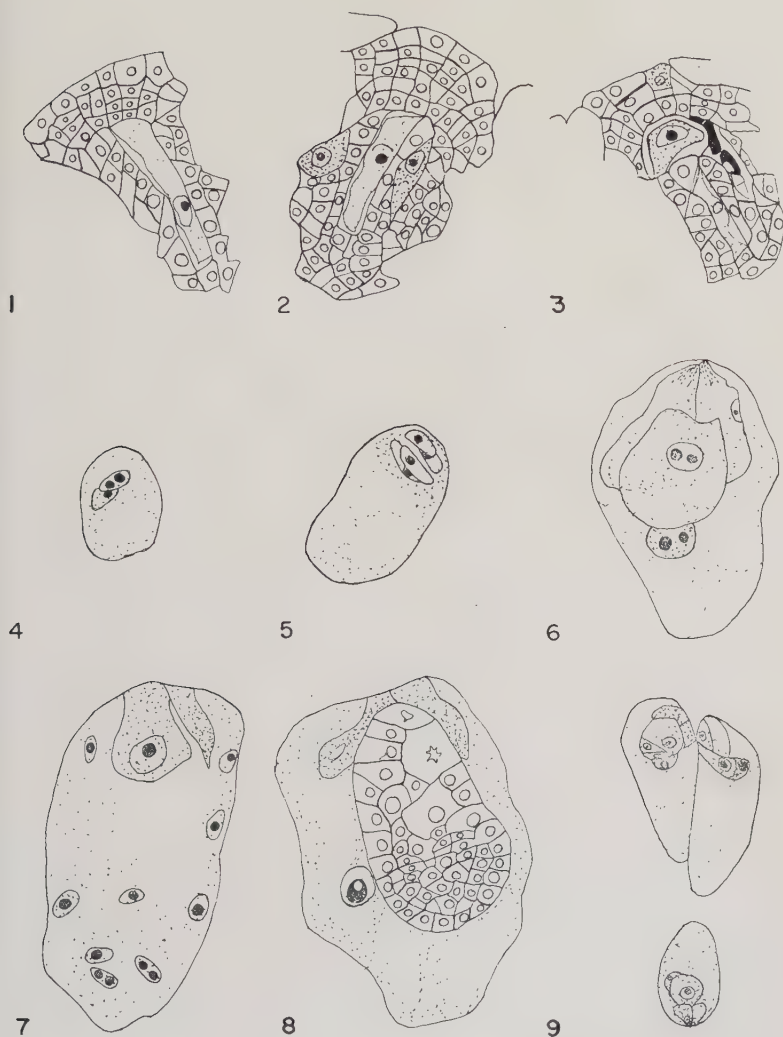
### OBSERVATIONS

All thirty-one plants from twenty-five different collections of *H. contortus* examined in this study were found to be aposporous apomicts. The apomictic mechanism involves the regular degeneration of the egg mother cell (EMC) (figs. 1, 2) not later than early prophase of meiosis, and the simultaneous or subsequent development of aposporous embryo sac initials (figs. 2, 3). No EMC division nor derivatives from such a division were observed in this study. The degeneration of the EMC appears to be dependent on factors inherent within the cell, since in many ovules degeneration occurs even in the absence of aposporous embryo sac initials (fig. 1). The EMC becomes less turgid, the cytoplasm becomes more granular and lighter staining. Finally the cell degenerates completely.

Following a period of enlargement and vacuolization, the nucleus of the aposporous embryo sac initial divides twice in rapid succession to produce four nuclei. These nuclei commonly remain in the micropylar end of the embryo sac (figs. 4, 5). As development of an embryo sac proceeds, the four nuclei usually organize into 4-nucleate, 4-celled embryo sacs, with 1 egg, 2 synergids, and 1 polar nucleus (fig. 6). Occasionally, however, 4-nucleate, 3-celled embryo sacs were observed containing 1 egg, 1 synergid, and 2 polar nuclei. No 8-nucleate embryo sacs were observed in the present material.

Many ovules of *H. contortus* produce only one aposporous embryo sac. In a majority of the ovules, however, two or more aposporous embryo sacs commonly develop. These embryo sacs appear to compete for the available space or nutritive supply, enlarging and encroaching upon each other as they develop.

The development of the embryo and endosperm begins shortly after, but apparently never prior to, anthesis. It was not determined if pollination is a prerequisite to development, but the appearance of pollen tube remnants in embryo sacs shortly after anthesis together with the subsequent development of embryos and endosperm strongly suggests that *H. contortus* is pseudogamous. Commonly the endosperm undergoes a num-



FIGS. 1-9. *Heteropogon contortus* (figs. 1-3, 6-9,  $\times 300$ ; fig. 4  $\times 440$  and fig. 5,  $\times 100$ ): 1, egg mother cell (EMC) starting to degenerate; 2, partially degenerate EMC and two developing aposporous embryo sac initials; 3, developing aposporous embryo sac initial at the apex of the nucellus and a portion of the degenerating EMC; 4, two-nucleate aposporous embryo sac with both nuclei in one end of the embryo sac; 5, the four-nucleate aposporous embryo sac; 6, a four-nucleate aposporous embryo sac organized with one egg, two synergids, and a single polar nucleus; 7, embryo sac showing the early development of endosperm prior to the initial division of the unreduced egg cell; 8, several-celled embryo and an undivided polar nucleus; 9, three aposporous embryo sacs of the same ovule showing development of a small mature four-nucleate sac in the chalazal region separated from the other two by several layers of nucellar tissue.

ber of divisions before the initial transverse division of the unreduced egg cell (fig. 7), but this pattern of development varies even within different ovules of the same inflorescence. Not infrequently embryos of 32–64 cells were observed “capped” at their apex by an undivided crescent-shaped, polar nucleus (fig. 8).

Although a majority of the aposporous embryo sacs develop in contact and later encroach upon one another, occasional ovules with multiple embryo sacs were observed in which the developing aposporous embryo sacs are relatively small, are separated by nucellar tissue, and develop to maturity without being encroached upon by other embryo sacs of the ovule (fig. 9).

The apomictic mechanism in *H. contortus* is one involving the regular production of 4-nucleate, aposporous embryo sacs followed by parthenogenesis. The complete failure of meiosis in megasporocytes of this species indicates that *H. contortus* is, or closely approaches, the condition of an obligate apomict.

## DISCUSSION

*Heteropogon contortus* is another species in the rapidly increasing list of grasses known to reproduce in whole or in part by agamospermy. *Heteropogon contortus* seems to be essentially an obligate apomict throughout its range, forming 4-nucleate, aposporous embryo sacs followed by parthenogenesis. It is obvious that, although *H. contortus* seems to be essentially an obligate apomict, variation within the species does arise, possibly through occasional hybridization, polyploidy, or chromosome loss. The occurrence of various chromosome forms, together with univalent and multivalent chromosome configurations in the microsporocytes, tends to indicate the probability of some intra- or inter-specific hybridization at one or more periods during the existence of the taxon. The possibility of sexual recombination during recent times is further suggested by the existence of diploid plants of *H. contortus* in India (Janaki-Ammal, 1946). Diploid relatives of aposporous apomicts are almost without exception sexual (Gustafsson, 1947).

The presence of diploid *H. contortus* in India, the fact that most Old World plants of the species have  $2n = 40$  and  $2n = 60$ , and that all New World plants have  $2n = 60$  or above would indicate that southern Asia might be the center of origin of the species. Southern Asia is considered to be the center of origin of the tribe Andropogoneae (Hartley, 1950). An Old World origin for the tribe is further indicated by the existence of numerous genera in the Old World that do not occur in the New, whereas there are no genera of New World Andropogoneae not present also in the Old World.

In most details the apomictic process in *H. contortus* is very similar to that reported by the authors (Brown and Emery, 1957) in *Themeda triandra* and *Bothriochloa ischaemum* of the Andropogoneae. The process



is also similar to that reported in species from various genera of the Paniceae, i.e., *Cenchrus* (Snyder, 1955), *Panicum* (Warmke, 1954), *Paspalum* (Smith, 1948), *Pennisetum* (Narayan, 1951), *Setaria* and *Urochloa* (Emery, 1957).

In both tribes (except, perhaps, for *Tripsacum* and *Saccharum*) 4-nucleate aposporous embryo sacs are produced following the degeneration of the sporogenous tissue. Pseudogamy appears to be characteristic of all apomicts in these two tribes. A minor difference in the process as it occurs in the two tribes seems to be the time of degeneration of the sporogenous tissues. In the Paniceae degeneration occurs during or just following the formation of megaspores. In the Andropogoneae the megasporocyte degenerates not later than early prophase of meiosis.

There are a number of aposporous grasses in other tribes of the family, but the process in them differs significantly from that in species of the Andropogoneae and Paniceae. In *Bouteloua curtipendula* (Chlorideae) four megaspores are produced by a very irregular apomeiotic division. The chalazal spore enlarges somewhat before it, like the other three spores, degenerates. The aposporous embryo sac is 8-nucleate (Brayant, 1952). In aposporous *Poa* species (Festuceae) the megasporocyte may complete meiosis and may form a functional reduced embryo sac. Whenever aposporous embryo sac initials are formed, however, they inhibit to some extent further development of the megasporocyte or spores. The aposporous embryo sacs produced are usually 8-nucleate when, and if, they reach maturity (Nygren, 1950). As far as known, therefore, the regular formation of 4-nucleate aposporous embryo sacs is restricted to the apomictic species of the Paniceae and Andropogoneae.

*Heteropogon contortus* is one of the very few grasses supposedly native to both the Old and New World tropics. Although varying greatly in the frequency of occurrence, the distribution of *H. contortus* is reported from every major land mass between 35°N. latitude and 35°S. latitude, and so far as can be determined from existing botanical literature, it is endemic in the New World, and in the Old World from South Africa to Australia, and numerous islands of the Pacific Ocean. The similarity of the apomictic process in clones from different parts of the species range suggests a common origin of the apomictic mechanism previous to the spread of the species throughout its present pan-tropical distribution. The alternative possibility is that apospory has arisen two or more times in isolated populations of the species and subsequently has developed to the same stage in each.

It is interesting to speculate on the possible age of apomixis in *H. contortus* since here is a highly successful, essentially obligate apomictic species, capable of establishing itself in climax grasslands of many regions. Parallel evolution of identical mechanisms for reproduction in various discontinuous and completely isolated populations seems unlikely in such a morphologically uniform species, and thus it may be con-

cluded that the development of apomixis in this species predates its trans-oceanic distribution.

If the pantropical distribution of *H. contortus* occurred in recent times, then the development of the apomictic mechanism in this species may also be a recent occurrence. If, on the other hand, its distribution occurred together with other tropical and sub-tropical floras, then the development of the apomictic mechanism may date back to the end of the Eocene epoch or earlier. The latter possibility would imply a very old species that, in spite of essentially obligate asexual reproduction, has spread widely and survived despite competition with sexually reproducing species in a variety of environments. There is no documentary evidence known to the authors indicating post-Columbian transfer from the Old World to the New or vice versa. Nevertheless, *Heteropogon* is one of the most highly specialized genera of the Andropogoneae and has two pan-tropical species. It is possible that its highly specialized spikelets, with their sharply barbed callus, may have permitted a recent pre-Columbian intercontinental migration.

In his extensive treatise on apomixis, Gustafsson (1947, p. 303) points out that the phytogeographical data on a number of distinct apomictic micro-species of glaciated regions seems definitely to prove the Old-Quaternary age of such taxa, and therefore, that the condition of agamospermy itself must have arisen in even more remote times. Apomixis in these species has existed, therefore, for somewhat more than one million years. This is the oldest estimate on the age of apomixis in extant species known to the authors, although Clausen (1954) states, "The facultative apomicts have exploited an extremely effective solution to these contrasting demands (referring to environment and species variability), a solution that enables them to store interspecific variability and to nevertheless remain constant for ages."

It appears reasonable that if apomictic microspecies of *Taraxacum*, *Hieracium*, and *Alchemilla* (cited by Gustafsson, 1947) have existed since the late Tertiary in a region of considerable environmental instability, then a definite possibility exists that an essentially obligate apomictic species might have endured under the more stable tropical and sub-tropical environments for a much greater period of time. The duration of apomixis in *Heteropogon contortus* may be short or very long; for the present it remains in the realm of speculation.

#### SUMMARY

1. Cytological studies of *Heteropogon contortus* (L.) Beauv. ex Roem. and Sult., a perennial forage range grass with an extensive range throughout most of the tropical and sub-tropical grassland regions of the world, revealed this species to be an essentially obligate, aposporous apomict with probable pseudogamous development of embryos.

2. The apomictic mechanism, as studied in twenty-five collections from various parts of the Old and New worlds, involves the regular degenera-

tion of the egg mother cell, initiation of one to several aposporous embryo sac initials, and, following two nuclear divisions in each sac, the organization of 4-nucleate aposporous type embryo sacs, these commonly with one egg, two synergids, and a single polar nucleus. Development of the embryo is probably pseudogamous, but is not dependent on the prior development of endosperm.

3. The close parallel between the apomictic mechanisms of *H. contortus*, *Bothriochloa ischaemum*, and *Themeda triandra* of the Andropogoneae and the reproductive mechanisms of previously reported aposporous apomicts of the Paniceae is pointed out.

4. Parallel evolution of identical apomictic mechanisms for reproduction in various discontinuous populations seems unlikely, and the authors conclude that the age of apomixis in *H. contortus* predates its trans-oceanic distribution. If this distribution were recent, then the age of apomixis in the species may be recent; but if the species were distributed as part of a tropical or a sub-tropical flora, then the age of apomixis may date back to the end of the Eocene epoch or earlier.

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IRIS, SECTION APOGON, SUBSECTION OREGONAE  
SUBSECT. NOV.<sup>1</sup>

QUENTIN D. CLARKSON

*Iris tenuis* Wats. is endemic to the upper Clackamas River and its tributary, Eagle Creek, in Clackamas County, northwest Oregon. A single specimen collected in 1884 from Washington County, Oregon, is apparently mislabeled, as the species has not been collected since from that area.

While the specific validity of *I. tenuis* has not been questioned, it has been included by authors in subsection *Californicae* of section *Apogon* only with some reluctance. Foster (1937) called attention to its morphological and cytological distinctions, but left it in the *Californicae*. Simonet (1934) placed the species in the *Sibiricae* mainly on cytological grounds, but Foster rejected this treatment for morphological reasons. Smith and Clarkson (1956) on the basis of cytological data proposed its removal from the *Californicae*.

Simonet reported a chromosome number of  $n=14$  for *I. tenuis*. Smith and Clarkson confirmed this number and also reported that fertile hybrids between other members of the *Californicae* are easily produced, but that hybrids could not be produced between *I. tenuis* and *I. tenax* Dougl. Presumably this barrier extends to other members of the subsection. Morphologically *I. tenuis* differs distinctively from other *Californicae* in having ensiform leaves and scarious instead of green bracts. Superficially, as Foster pointed out, it resembles *I. cristata* Ait., and the general appearance of the species is unlike other *Californicae*.

Inclusion with the *Sibiricae*, as proposed by Simonet, seems unwise not only because of morphological differences but also because of geographical considerations. If *I. tenuis* is placed with the *Sibiricae* it becomes an isolated member of the subsection with little in common except a possible base chromosome number of  $n=7$ .

<sup>1</sup> Grateful acknowledgment is made to Sister John Mary of Marylhurst College for her assistance with the Latin diagnosis and to Dr. Helen Gilkey of Oregon State College for her helpful comments.

Regardless of origin, *I. tenuis* is sufficiently distinct, morphologically, cytologically, and geographically, to warrant erection of a new subsection which is accordingly proposed.

IRIS, sect. APOGON, subsect. **Oregonae**, subsect. nov. Perennes ex rhizomis gracilibus; folia ensiformia, subviridia, basibus scariosis, equitantes; caulis ramosus, 2–3 flores in omni ramo; spathae scariosae, oppositae, unifloriferae; perianthii tubus pedicellusque breves; flores pallide albi aut caeruleo-tincti.

Perennials from slender rhizomes; leaves ensiform, pale green, scarious at base, equitant; stems branched, 2–3 flowers on each branch; spathes scarious, opposite, 1-flowered; perianth tube and pedicel short; flowers pale white or tinged with blue. Type species. *I. tenuis* Wats. Proc. Amer. Acad. XVII: 380. 1882.

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#### REVIEWS

*How to Identify Plants.* By H. D. HARRINGTON. 203 pp., illustrated by L. W. Durrell. Sage Books. 1957. Denver, Colo. \$3.00.

This handy, pocket-sized "how-to-do-it" book, by the author of the Manual of the Plants of Colorado, is designed "to provide practical help for those interested in learning the special technique of identifying plants." It is printed by offset and has numerous, simple line drawings. The more common descriptive terms are grouped into eight chapters, each chapter devoted to a particular category of structure, e.g., flower, stem, leaves. The student is advised to commit these terms to memory, whereas terms less commonly used are included in a 79-page, partly illustrated glossary for reference, at the end of the book. Although the definitions are said to be based on usage in the "average manual," "cell" is eschewed for "locule," and one might wish that the term "pistil" had been avoided also, because it is difficult to homologize with the idea of sporophylls (page 29, fig. 46). A key is offered to the characters of leaf surface, and another to common types of fruit; in the latter the use of both "pistil" and "carpel" seems needlessly confusing. A special chapter on the use of keys, including synoptical, bracket, and indented types, contains useful comments on difficulties likely to be encountered and means of overcoming them. Collecting and preparing specimens are described succinctly; the collector is not told how to retain the association between data and specimens after the latter have been kept "all day" in a vasculum or lard can! A useful feature is a series of five outline maps showing the geographical coverage of the principal manuals and floras of the United States and North America; it is unfortunate, however, that references to three useful floras are omitted from maps I and II—Jepson, W. L. Manual of the flowering plants of California; Kearney, T. H., and R. H. Peebles, Arizona Flora; and Tidestrom, I. Flora of Utah and Nevada.

Judged strictly within its avowed limitations, this small volume should prove a useful teaching aid in both field and laboratory.—LINCOLN CONSTANCE.



## NOTES AND NEWS

INDEX TO PLANT CHROMOSOME NUMBERS. The need for up-to-date coverage of the literature dealing with plant chromosome numbers has led to an undertaking designed to compile and publish in annual installments a chromosome index for the entire plant kingdom.

This is being done by a group of botanists who are reviewing some two hundred journals and are listing all original chromosome counts occurring therein, except those resulting from endopolyploidy or deviating because of experimental treatment.

The Index, compiled from the journals of a single year, will be published annually within the shortest possible time after the last issue of each journal is available. In addition, there is planned a supplement containing counts published in previous years, but hitherto not indexed. Each issue of the Index will contain a complete bibliography for the counts included in that number.

The Index is published by the California Botanical Society. The first issue, supported by grants from the University Research Council of the University of North Carolina, and the National Science Foundation, went to press in May, 1958. It covers the 1956 journals, from which over 2000 listings have been taken. Produced by offset process on  $8\frac{1}{2} \times 11$ -inch paper, and punched for loose-leaf binders, it is priced at \$1.00. Orders (except from libraries and institutions) must be accompanied by payment and may be sent to C. Ritchie Bell, Department of Botany, University of North Carolina, Chapel Hill, North Carolina.

Further information can be obtained from Marion S. Cave, Research Associate, Department of Botany, University of California, Berkeley 4, California.

Some publications of interest follow:

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